BIOLOGY

Soil Respiration on the Volcanic Island Surtsey, Iceland in 1987 in Relation to Vegetation

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ABSTRACT

Soil respiration at three different stages of vegetation development was measured in the *Honkenya peploides/Elymus arenarius* community in Surtsey over a three day period in July. The soil respiration rate was lowest (88 mg CO_2 m^{-2} hr^{-1}) in a plot bare of vegetation, slightly higher (110 mg CO_2 m^{-2} hr^{-1}) in a plot dominated by *Honkenya,* but consistently highest (281 mg CO_2 m^{-2} hr^{-1}) in a plot dominated by *Elymus.* Soil properties were similar in the three plots and the respiration rates were related to differences in vegetation cover and root biomass between the plots. Root biomass was found to be relatively low and the organic carbon and nitrogen status of the soil poorly developed.

INTRODUCTION

Surtsey has provided scientists with an unique opportunity to follow biological succession in a terrestrial habitat devoid of life and organic substances in its first stage of formation. Since the eruptions came to an end in 1967 the development of life on the island has been uninterrupted. Early investigations revealed that the fresh volcanic substrate became contaminated with microbial algae, bacteria and moulds within a relatively short time and biologcal activity was established on the island (Schwabe 1970, Smith 1970, Fridriksson 1975). The first vascular plant was found growing on Surtsey in 1965 (Fridriksson 1966), bryophytes became established in 1967 (Jóhannsson 1968) and lichens were first detected in 1970 (Kristinsson 1972). Plants play a key role in soil formation processes, one of the greatest contributions being the addition of organic matter to the soil upon which the decomposer communities are founded.

On Surtsey nitrogen-fixation by blue-green algae has been demonstrated under a variety of conditions (e.g. Henriksson & Rodgers 1978), but their ecological importance in the development of life on the island has been debated (Brock 1972, Henriksson & Henriksson 1982). Development of bryophytes and lichens has been rather slow on Surtsey due to unfavourable substrate conditions. Although they may be locally abundant they have not contributed significantly to the formation of plant cover on the island. The advancement of the vascular plant colonization on Surtsey has, on the other hand, been steady (Fridriksson 1987) and is probably of greatest importance in the establishment of vegetation and soil biota on the island.

The objective of the present study was to investigate the biological activity and soil properties in an area of Surtsey where plant colonization is in a relatively advanced stage of succession. For this purpose measurements of soil respiration were carried out on the island. Soil respiration has been defined as "the sum total of all soil metabolic functions in which CO_2 is produced" (Singh & Gupta 1977). The rate of CO_2 evolution from soil surfaces has been commonly used to measure soil respira-

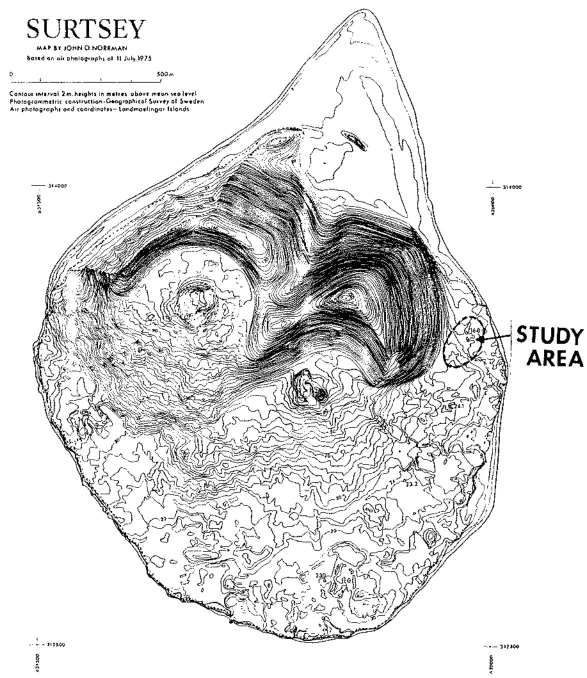

Fig. 1. Location of the study area on Surtsey.

tion. The main source of CO_2 evolving from the soils of most terrestrial ecosystems are microbial, microfaunal and root respiration. Studies of soil respiration have been used to measure and compare soil metabolism in different ecosystems or successional stages within the same ecosystem.

STUDY AREA

The study was conducted on the easternmost part of the island (Figure 1) in an area where windblown tephra and sand has filled the depressions in the underlying lava and levelled the terrain. The area is between 10 and 20 m a.s.l. On this part of the island the vegetation was most developed. The area was invaded by vascular plants in 1968 when the first young plants of *Honkenya peploides, Elymus arenarius* and *Mertensia maritima* were found there (Fridriksson 1975). Of these species only *Honkenya* persisted in the area from the first year of discovery, but *Elymus* and *Mertensia* did not gain a foothold there until 1973 (Fridriksson 1978). The three species have produced seeds and increased in numbers. The population growth has been most prolific in *Honkenya* and it was the most prominent species in the study area in 1987. *Elymus* has also increased considerably in numbers and the oldest plants have formed small sand dunes in association with *Honkenya* plants (Fridriksson 1982). Of *Mertensia* there were only a few scattered plants. Estimations of vegetation cover in the area in 1987 indicated an average plant cover of 8.5%, all of which was attributable to *Honkenya* plants (Fridriksson 1991). Conditions for bryophytes and lichens are poor in the area and they were of no ecological significance in the development of the plant community.

Three study plots representing different stages of vegetation development on the tephra soil were selected for the soil respiration measurements. The plots were distanced approximately 40–150 m apart.

a) Bare plot

The plot was considered as a base-line reference and for it a nearly unvegetated patch within the study area was selected. There were neither mature plants within the plot nor in the immediate viscinity of it. Four small *Honkenya* plants, probably in their second year, with only one shoot each were found within the plot and sixteen seedlings of the same species. One young *Elymus* plant, with stolon and 3 leaves, was also found within the plot. The size of the plot was 15×1 m.

b) *Honkenya* plot

The plot was located in an area considered to be representative of a well developed *Honkenya* colony. In the plot there were numerous mature *Honkenya* plants as well as young plants in their first and second year. One immature *Elymus* plant with nine leaves, and six seedlings of the same species were found scattered within the plot. The size of the plot was 15×1 m.

c) *Elymus* plot

The plot transected the center of a sand dune formed by the largest *Elymus* plant (No. 74-51) growing on Surtsey in 1987. The plant was first recorded on the island as a seedling in 1974 (Fridriksson 1978). In 1979 the plant produced seeds for the first time and in that year it occupied an area of 155x290 cm (Fridriksson 1982). In 1987 the plant covered a circular area with a diameter of about 650 cm. In the dune several *Honkenya* plants grew in association with the *Elymus*. In the center the dune had reached a height of approximately 120 cm above its surroundings. For several years a pair of Great Black-backed Gulls (*Larus marinus*) has bred in the dense *Elymus* cover of the

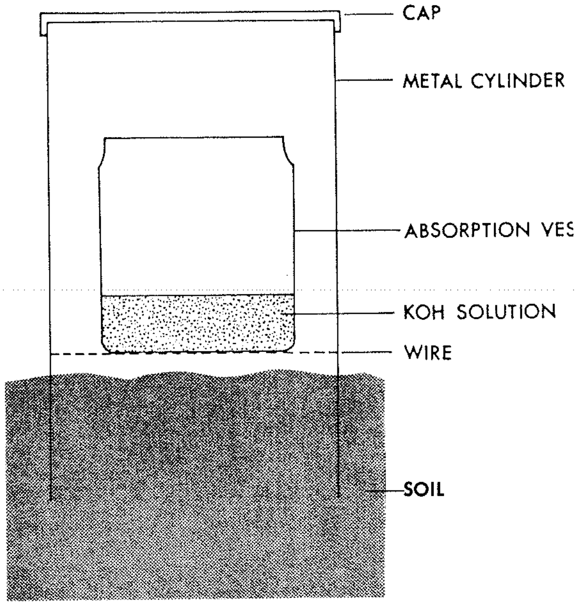

Fig. 2. Schematic drawing of apparatus used to measure soil respiration in the field.

dune and in 1987 the young had recently left the nest when the respiration measurements were carried out. The size of the plot was reduced to 10×1 m in order to match somewhat better the size of the dune.

METHODS

Soil respiration

Carbon dioxide evolution from the soil was determined by using an alkali absorption method (Gupta & Singh 1977). Open ended metal cylinders 10 cm in diameter and 18 cm high were inserted 5 cm into the soil. Green plant material was removed if it occurred within the cylinders. A wide-mouthed glass jar containing 50 ml of 0.2M KOH solution was placed into the cylinders for absorption of CO_2. A wire inside the cylinders kept the jars about 2 cm above the soil surface so they did not interfer with CO_2 evolution from the soil (Figure 2). The cylinders were sealed and left in the ground for 24 hours at a time. Four replicates were used and cylinder positions were randomly selected at the beginning of each 24 hour period. To serve as controls, four cylinders open at one end, and of the same volume above ground as in the active cylinders, were used and these were handled in the same way as the active cylinders. At the termination of each measurement period the alkali solution was poured from the glass jars and into air-tight plastic bottles, in which it was kept until analysis was carried out in the laboratory. The respiration measurements were run for three consecutive days, starting with the first 24 hour period in the afternoon of 2nd of July.

CO_2 absorption was analyzed by titrating the unneutralized KOH with diluted standardized 0.200N HCl after precipitation of the carbonate with excessive (15 ml) 3N $BaCl_2$ and using phenolphthalein as an indicator. The following formula was used to calculate the amount of CO_2 evolved:

$$\text{mg } CO_2 = (B - V)\, N\, E$$

where: V = volume of acid required to titrate the KOH in the active cylinders to the end point; B = volume of acid to titrate KOH in the control cylinders to the end point; N = Normality of HCl; E = equivalent weight, E = 22 if the data are expressed as CO_2 (Strotzky 1965, Magnússon 1986). For each sample the results were converted and expressed as mg CO_2 m^{-2} hr^{-1}. The capacity of the solution used was to absorb 220 mg of CO_2, which is equivalent to 1167.1 mg CO_2 m^{-2} hr^{-1} over a 24 hour period.

Although the alkali absorption method may underestimate CO_2 release it has been found to be well suited for measuring soil respiration due to the relatively simple apparatus used and low cost, which enable extensive replication of measurements in a variety of habitats (Coleman 1973, Singh & Gupta 1977). The results obtained by the method may therefore not give absolute values but rather be a relative measure of the intensity of soil respiration. Such data can however be useful in comparing respiration under different conditions (Reiners 1968).

Soil moisture, temperature and chemistry

For determination of soil moisture, surface samples 14.5 cm deep × 3.5 cm in diameter, were taken underneath the respiration cylinders at the termination of each 24 hour measurement period. The samples were sealed in plastic bags and stored until handled in the laboratory. Moisture content was determined gravimetrically after drying the samples at 80°C for 48 hours, and calculated as % dry weight.

Soil temperature was measured with a maxima-minima thermometer, which was placed horizontally into a 15 cm deep soil pit and covered with the displaced soil. The pit was made outside the study plots and within a 1 m distance of them. Measurements were only made by the bare plot and the *Honkenya* plot. After each 24 hour period, the thermometers were recovered and after reading were reset and put back in place.

The soil samples collected for soil moisture determination after the second 24 hour period of respiration measurements were analyzed for pH and content of organic carbon, nitrogen and potassium. The dried samples were sieved through a 0.5 mm mesh. Measurements of pH were made in a mixture with distilled water, content of organic carbon (C%) by Walkley-Black titration (Jackson 1958), nitrogen (N%) using the Kjeldahl method, and potassium (K) with 1.25% acetic acid suspension and flame photometry.

Plant cover and root biomass

The plant cover was determined using the line-intercept method. Within each study plot a meter tape was laid out twice along the plot at a 33 cm and 66 cm distance from the side line. Plant species that intercepted the line were recorded to the nearest 1 cm. The accumulated length out of the total tape length occupied by plants was used to express percentage cover.

After all soil respiration measurements had been completed, the study plots were divided into four equal parts of 1 m width. In the center of each part the respiration cylinders (10 cm diameter) were driven 20 cm into the soil. All soil and root material within the cylinders was then removed and put on a sieve with a 2 mm mesh size. From the sieve all visible roots were collected and placed in plastic bags. In the laboratory the weight of the root samples was determined by ignition at 600°C for 2 hours. This method was selected due to the difficulties involved in detatching small tephra-grains from fine roots which was considered to result in a loss of root material.

Statistical analysis

The data were subjected to analysis of variance, and means checked at $p=0.05$ level of significance.

CLIMATE

Surtsey, being the southernmost terrestrial part of Iceland, has a rather mild, oceanic climate. At the Vestmannaeyjar meteorological station on Stórhöfdi, Heimaey, which is 22 km northeast of Surtsey, the mean annual temperature during 1931–1960 was 5.4°C. The mean January temperature was 1.4°C and the mean July temperature 10.3°C, which were the coldest and warmest months respectively. The annual precipitation for the same period was 1402 mm. In the driest months (May and June) the mean precipitation was 81 mm, but 156 mm in the wettest month (December) of the year (Einarsson 1976). Meteorological observation on Surtsey in 1967 and 1968 indicated that the climatic conditions on the island do not deviate markedly from those of Stórhöfdi (Fridriksson 1975).

In 1987 the monthly temperature on Stórhöfdi in April, May and June was near the 1931–1960 average. In April and May the monthly precipitation was above average, but June, on the other hand, was extremely dry with a precipitation of only 12.3 mm (Vedráttan 1987). The temperature at Stórhöfdi during the time of the soil respiration measurements on Surtsey on July 2–5 appears to have been near normal (Icelandic Meteorological Office, unpublished records), but the precipitation records indicate a dry period (Table 1).

Meterological measurement were not carried out on Surtsey in 1987, but the following was noted during the stay on the island:

July 2. Calm, cloudy and dry, soil surface dry on arrival at 10.30. Slight rain around noon, but otherwise dry and calm for the rest of the day.

July 3. Started raining at about 00.30 and continued during the night. Eastern breeze, cloudy and dry during the morning, became calm and sunny in the afternoon and evening.

TABLE 1.
Mean daily air temperature and total precipitation during June 26–July 5, 1987 at Stórhöfdi, Heimaey

Day	Temperature °C	Precipitation mm 24 hours
26.6	7.8	0
27.6	7.2	0
28.6	7.9	0
29.6	8.7	trace
30.6	10.8	2.3
1.7.	9.6	0.3
2.7.	9.7	0
3.7.	10.4	trace
4.7.	11.5	0
5.7.	10.2	1.0

July 4, clear and calm during the night. Northwest breeze and sunny during the morning and early afternoon. Became cloudy around 17.00. Slight rain in the evening.

July 5. Rained intermittently during the night and morning. Continuous rain in the afternoon. Wind calm.

RESULTS

The soil respiration rate in the plots ranged from 79.6 to 381.7 mg CO_2 m^{-2} hr^{-1}. The rate was on all days consistently highest in the *Elymus* plot and significantly different from the rates determined in the bare plot and the *Honkenya* plot, which did not differ significantly from each other (Table 2). In the bare plot, however, the respiration rate was lowest on all days. Over the three day period the mean respiration rate was 1.26 and 3.20 times higher in the *Honkenya* and *Elymus* plots respectively, than the rate in the bare plot. There was no consistent change in respiration between days in the different plots. In the bare plot and the *Honkenya* plot there was little spatial and temporal variation in respiration rate. In the *Elymus* plot there was, on the other hand, a considerable variation in this respect, and it was also noted that the respiration rate was higher in the part of the plot which had *Elymus* cover than in spots which were bare of vegetation or had *Honkenya* cover only. The difference in respiration rate between days in the plot coincided with the number of respiration cylinders positioned within the *Elymus* cover, which was 3, 1 and 2 on days 1, 2 and 3 respectively. Over the three day period the respiration rate of the cylinders within the *Elymus* cover averaged 414.0 mg CO_2 m^{-2} hr^{-1}, while the rate of those outside it in the same plot was 148.4 mg CO_2 m^{-2} hr^{-1}.

The soil moisture content ranged from 6.24 to 9.45 dry weight (Table 2). The soil samples lost on the average 10.81 g of weight upon drying, which corresponds to 7.75% of the soil volume sampled being filled with water. The moisture content was lowest in the bare plot and significantly different from that in the other plots. There was a significant decline in moisture content of the soil over the three day period.

The soil temperature at 15 cm depth fluctuated between a minumum of 12.0°C and a maximum of 27.5°C (Table 2). The temperature rose over the three day period, which appeared to reflect the changes in air temperature at Stórhöfdi (Table 1) and a shift from cloudy to sunny weather on Surtsey during the measurements.

The soil chemistry analysis gave similar results between plots for pH and content of carbon and potassium (Table 2). The concentration of these elements was, however, highest in the *Elymus* plot, but the difference was not significant. The nitrogen content of the soil in the *Elymus* plot was, on the other hand, significantly higher than that of the other plots.

Plant cover was not measureable in the bare plot, but in the *Honkenya* plot and the *Elymus* plot respectively 13.2% and 70.6% of the soil surface was covered with vegetation (Table 2). In the *Honkenya* plot all the vegetation cover

TABLE 2

Soil respiration rates, moisture, temperature, plant cover and root biomass under three different vegetation conditions in Surtsey in 1987. Values are x±S.E. for respiration, moisture, chemistry variables and root biomass, N=4.

Plot	Bare	*Honkenya*	*Elymus*
Soil respiration mg CO_2 m^{-2} hr^{-1}			
Day 1 (July 2–3)	79.6±12.2	122.2±10.5	381.7±104.4
range	52.2–110.8	103.1–147.7	132.6–583.1
Day 2 (July 3–4)	85.9±4.4	101.5±2.0	170.9±45.5
range	73.9–94.2	98.0–107.0	98.0–287.7
Day 3 (July 4–5)	98.0±3.8	107.6±5.0	290.9±66.0
range	90.4–105.7	96.8–118.4	137.5–407.4
Day 1–3 mean	87.8	110.4	281.2
Soil moisture % dry wt			
Day 1	7.75±0.59	8.38±0.58	9.45±1.06
Day 2	6.99±0.44	8.30±0.15	8.13±0.70
Day 3	6.24±0.52	7.68±0.28	7.28±0.63
Soil temperature °C -15 cm, min-max			
Day 1	12.0–19.0	14.0–17.0	n.d.
Day 2	13.5–24.5	14.5–20.5	n.d.
Day 3	15.0–27.5	14.5–27.5	n.d.
Soil chemistry			
pH	7.0±0.1	6.9±0.1	7.1±0.1
C% dry wt	0.23±0.03	0.23±0.01	0.28±0.01
N% dry wt	0.008±0.003	0.011±0.002	0.033±0.008
K meq 100 g^{-1}	0.31±0.01	0.30±0.03	0.47±0.08
Vegetation			
Plant cover (%)	0	13.2	70.6
Root biomass g m^{-2} 0-20 cm	0	14.5±5.0	45.9±17.7

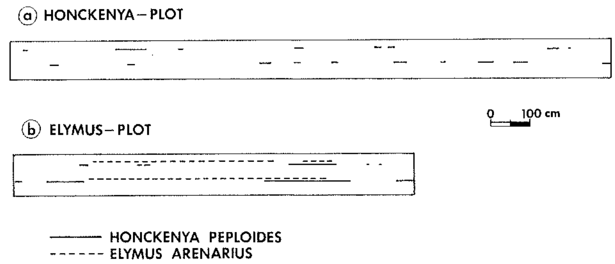

Fig. 3. Occurrence of plants along two longitudinal line-transects in the vegetated study plots on Surtsey, where soil respiration was determined.

was attributable to *Honkenya* plants, which were distributed throughout the plot (Figure 3). In the *Elymus* plot, the total cover of *Elymus* was 56.2%, while that of *Honkenya* plants was 26.6%. Some of the *Honkenya* in the plot formed a layer underneath the *Elymus* cover, which explains the difference in total plant cover and the additive cover of the two species (Figure 3).

Roots were not detected in the soil samples in the bare plot, but in the *Honkenya* plot root biomass was estimated by ignition as 14.5 g m^{-2} in the top 20 cm of the soil, and 45.9 g m^{-2} in the *Elymus* plot. The means were significantly different. The proportional variation in root biomass between samples was similar in both plots (Table 2).

DISCUSSION

The soil respiration rates, 80–382 mg CO_2 m^{-2} hr^{-1}, determined in Surtsey were within the range reported in various studies of soil respiration in dry grassland and open habitats, which vary from 0 to over 1100 mg CO_2 m^{-2} hr^{-1} depending on the season (Walter & Haber 1957, Lieth & Quellette 1962, Kucera & Kirkham 1971, Coleman 1973, Chapman 1979, Gupta and Singh 1981, Parker et al. 1983). The rates from Surtsey are high in comparison to the results of Lieth & Quellette (1962), who reported a soil respiration rate of 57 mg CO_2 m^{-2} hr^{-1} in July in a *Elymetum arenarii* community on gravelly sand, along the sea coast of the Gaspé Peninsula in Quebec, Canada. In other dry open communities the rate was in the range of 55 to 141 mg CO_2 m^{-2} hr^{-1}. The soil respiration rates reported by Walter & Haber (1957) from Germany were, on the other hand, closer to the results of the present work. In a sand dune without vegetation on the Rhine the soil respiration rate was 89 mg CO_2 m^{-2} hr^{-1} in July, and in an *Agrostis* meadow on sand the rate was 315 g CO_2 m^{-2} hr^{-1} during July to October. The soil respiration rates measured by Chapman (1979) in a lowland *Calluna* heathland developed on sand dunes in southern England were considerably higher than the rates observed on Surtsey, but at a soil temperature of 10–18°C they ranged from approximately 220 to 950 mg CO_2 m^{-2} hr^{-1}.

The difference in soil respiration rate between the three plots studied in Surtsey presumably reflects their vegetation condition. The observed variation in moisture content, temperature and chemistry of the soil between the plots was minor and did not correlate well with the soil respiration rate, which the vegetation variation, however, did. The respiration rate measured in the bare plot was relatively high, taking into account that no roots were extracted from the soil within the plot and the absence of surface litter, the low organic matter content and low status of microbial and faunal activity og the tephra soil in Surtsey (Henriksson & Henriksson 1974, Henriksson & Rodgers 1978, Broady 1982, Bödvarsson 1982, Ólafsson 1982). The soil is probably well aerated near the surface due to its low organic matter content, relatively coarse particle size and low water holding capacity. Therefore diffusion of atmospheric CO_2 into the soil and uptake in the respiration cylinders may have occurred and could explain to some extent the high respiration rates measured in Surtsey. Assuming that the CO_2 uptake in the bare plot represents mostly non-biological sources of CO_2 in these soils, then the average soil respiration rate over the three day period would be about 20 and 190 mg CO_2 m^{-2} hr^{-1} in the *Honkenya* and *Elymus* plots, respectively. Further studies are, however, needed to verify this.

In Surtsey, the roots and the associated rhizosphere micro-organisms were probably the primary sites of biological activity in the soil and sources of respiratory CO_2. A build up of a litter layer at the surface has not occurred in the young and exposed habitat and the organic matter content of the soil is extremely low, and therefore the contribution from these sources to that total soil respiration is probably still negligible. Estimates of contribution of root respiration to total soil respiration vary considerably (Chapman 1979), which reflects both differences in methodology as well as in the plant communities and soil types studied.

Phillipson et al. (1975) attributed only 3–4% of soil respiration to roots in a beechwood, while Chapman (1979) estimated root respiration as 70% of total soil respiration in a *Calluna* heathland. The root biomass, 14-46 g m^{-2}, in the young plant community in Surtsey was relatively low in comparison to results of studies from grasslands and dry open habitats, where root biomass has been determined to be in the range 100 to 1900 g m^{-2} (Perkins et al. 1978, Richards 1986). It must, however, be borne in mind that sampling of roots below 20 cm was not carried out in Surtsey.

The study showed that the tephra soil of Surtsey has the characteristics of immature soils, as was expected. In freely drained grassland soils in Iceland the pH is commonly 5.4–6.3, orgainc carbon ranges from 5–15% and nitrogen from 0.4–0.8% (Helgason 1968). Studies of the properties of soils of denuded highland areas in Iceland (Arnalds et al. 1987) indicate that they are somewhat lower in pH and richer in organic carbon and total nitrogen content than the soils of Surtsey. The carbon and nitrogen status of the soil in Surtsey was similar to that found in soils of mobile coastal dunes with a *Elymo-Ammophiletum* community in southern Norway (Lundberg 1987), which have a very low organic, nitrogen and moisture content in comparison to the soils under the communities of the older fixed dunes. Studies of succession on dunes in Britain have shown that a build up of soil organic content is a very slow process and centuries rather than decades are needed for distinct changes to occur (Chapman 1976). The total nitrogen concentrations determined in the soil in Surtsey in the present study are within the range found in studies on the island in 1974 and 1976 (Henriksson & Rodgers 1978), which indicates that the nitrogen status of the soil has not improved markedly over the last ten years.

The soil in the *Elymus* plot was richer in nitrogen than the soil of the bare plot and the *Honkenya* plot, and also its carbon and potassium content was relatively high. It is probable that the higher nutrient status in the *Elymus* plot was due to the effects of bird faeces and food remains from the pair of nesting gulls in the dune, rather than to the difference in vegetation development. The enrichment of the soil by the birds may also have affected the biological activity of the soil directly and the soil respiration rate in the plot. In recent years there has been a considerable increase in the number of breeding gulls on Surtsey, in particular Lesser Black-backed Gulls (*Larus fuscus*) and Herring Gulls (*Larus argenteus*), which nest in colonies and revisit them year after year. Defecation has been shown to be of importance in enhancing soil-nutrient concentrations in Herring Gull colonies (Sobey & Kenworthy 1979). The breeding birds may in the future have profound effects on the rate of vegetation development and soil formation on Surtsey.

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